Systematics of the Troglobitic *Caecidotea* (Crustacea: Isopoda: Asellidae) of the Southern Interior Low Plateaus

JULIAN J. LEWIS

Department of Biology and Water Resources Laboratory, University of Louisville, Louisville, Kentucky 40292

ABSTRACT.— *Caecidotea meisterae* is synonymized with *Caecidotea whitei*, which is reduced to a subspecies of *Caecidotea bicrenata*. This species is now divided into two subspecies: *Caecidotea bicrenata bicrenata* and *Caecidotea bicrenata whitei*. *Caecidotea b. bicrenata* occurs in caves from northern Alabama to central Tennessee. From northern Tennessee to southern Illinois it is replaced by *C. b. whitei*.

Fleming (1972a), following Bresson (1955) and Steeves (1963; 1964), considered *Caecidotea alabamensis* Stafford (1911 to be a widespread troglobite inhabiting caves of practically the entire Interior Low Plateaus, from Alabama to Indiana and Illinois. Lewis and Bowman (1981) pointed out the morphological and zooeographical dissimilarities of *C. alabamensis* to species occurring in caves of the Interior Low Plateaus, restricting the known distribution of *C. alabamensis* to the type-locality, Auburn, Alabama. *Caecidotea jordani* (Eberly) was resurrected for a distinct species in central Indiana, as was *Caecidotea bicrenata* (Steeves) for the troglobitic species in northern Alabama. Three new species closely related to *C. jordani* and *C. bicrenata* were described by Lewis and Bowman (1981) to encompass "*alabamensis*" collections from southern Illinois, Kentucky, and northern Tennessee. These were *Caecidotea beattyi*, *Caecidotea meisterae*, and *Caecidotea whitei*.

Additional information now necessitates modification of part of the scenario of Lewis and Bowman (1981) for the "*alabamensis*" species. While that paper was in press, collecting in Mammoth Cave National Park produced both *Caecidotea whitei* and *C. meisterae,* in addition to *Caecidotea stygia*. The presence of both *C. stygia* and *C. whitei* in the ecologically complex Mammoth Cave System was explained by Lewis and Lewis (1980). However, the presence of three species stretched credence, pointing to the possibility that *C. meisterae* and *C. whitei* are conspecific.

Study of numerous specimens from the base level cave rivers of the Mammoth Cave System revealed intergradations between specimens with the weakly developed gnathopods of *C. whitei* and those with the more fully differentiated gnathopods of *C. meisterae*. As the morphology of the gnathopods was the primary character used to distinguish these two species, it became apparent that they were identical.

A gray area left unconsidered by Lewis and Bowman (1981) was central Tennessee, where numerous collections previously called "*alabamensis*" were assigned neither to *C. bicrenata* nor any of the new

species. Examination of many collections showed that *C. bicrenata's* range extends from northern Alabama to north central Tennessee. In northern Tennessee and southern Kentucky *C. whitei* occurs, continuing north to Hart County, Kentucky, and west into southern Illinois. The only substantial morphological difference between *C. bicrenata* and *C. whitei* is the shape and placement of the lateral process of the male second pleopod endopod tip. Although this difference in morphology is consistent, other distinguishing characteristics are too variable to be reliable. Furthermore, significant dispersal barriers that might provide reproductive isolation do not appear to exist along the boundary between the ranges of *C. whitei* and *C. bicrenata.*

Caecidotea meisterae is herein synonymized with *Caecidotea whitei,* and *C. whitei* reduced to a subspecies of *Caecidotea bicrenata.* The rest of the taxonomy proposed by Lewis and Bowman (1981) for other "*alabamensis*" species, i.e., *Caecidotea antricola, C. beattyi* and *C. jordani,* remains unchanged.

Caecidotea bicrenata bicrenata, new status.

Asellus alabamensis. — Bresson, 1955:51-59, 65, 70. — Chappuis, 1957:39, 41-42, (in part, *C. antricola* Missouri specimens). — Steeves, 1964:503-504; 1966:394-396, 401-402; 1969:521. — Barr, 1967:190-191. — Cooper and Cooper, 1968:22. — Fleming, 1972a: 230-231, 245-247 (Alabama records); 1972b:498; 1973:287-291, 294, 300, 302-303.

Asellus bicrenatus Steeves, 1963:471, 474-476, 478, 480.

Conasellus alabamensis. — Henry and Magniez, 1970:356.

Material examined — ALABAMA: *Colbert Co.*, Cobbs Bear Pit Cave, 25 Oct 1969, F. Shires and R. Cobb, 3♂♂, 1♀. *Jackson Co.*, Flatworm Cave, 7 May 1969, R.C. Graham, 2♂♂, 3♀♀; New Fern Cave, W. Torode, July 1969, 5♂♂. *Marshall Co.,* Beech Spring Cave, July 1969, W. Wilson, R.C. Graham, 4♂♂, 3♀♀; Off Limits Pit Cave, Feb 1971, R.C. Graham, 1♂, 2♀♀. *Morgan Co.,* B & J Cave, 23 July 1970, W. Torode, 7♂♂, 6♂♂. TENNESSEE: *Bedford Co.,* Reese Cave, 8.6 mi. S Shelbyville, 22 Dec 1956, L. Hubricht, 1♂, 7♀♀. *Cannon Co.,* cave 3.5 mi. SSW Bradyville, 21 Aug 1967, S. Peck, A. Fiske, 1♂, 1♀; Fisher Cave, 1 July 1973, S. Peck, 1♂, 2♀♀; Ten Penney Cave, 2 mi. NW Woodbury, 9 Sep 1967, S. Peck, A. Fiske, 2♂♂, 3♀♀. *Davidson Co.,* Brents Cave, 18 Nov 1956, T.C. Barr, 3♂♂, 23♀♀. *DeKalb Co.,* Ted Cave, 5 mi. E Smithville, 29 Aug 1939, L. Hubricht, 12♂♂, 13♀♀. *Franklin Co.,* Caroline Cove Cave, 5.5 mi. SE Belvidere, 11 July 1967, S. Peck, A. Fiske, 7♂♂, 20♀♀; Lost Cove Cave, 5 mi. N Sherwood, 27 Aug 1968, S. Peck, 3♂♂, 10♀♀; Pitcher Ridge Cave, 6 mi. N Hytop, 19 Aug 1967, S. Peck, A. Fiske, 2♂♂, 3♀♀; Putnam Spring Cave, 9 mi. S Belvidere, 19 July 1967, S. Peck, A. Fiske, 7♂♂, 7♀♀; seep, 3.8 mi. N Sherwood, 9 May 1954, L. Hubricht, 18♂♂, 5♀♀; seep, 6.5 mi. S Sewanee, 23 May 1961, L. Hubricht, 7♂♂, 6♀♀, *Marion Co.,* Crystal Cave, Monteagle, 17 Mar 1931, collector unknown, 1♂. *Rutherford Co.,* Echo

Cave, 1.2 mi. N Rockvale, 22 Oct 1956, T.C. Barr, 1♂, 7♀♀; Rainbow Cave, 2.3 mi. SW Walter Hill, 1 June 1941, L. Hubricht, 2♂♂, 5♀♀. *White Co.,* Haskell Cave, 2 mi. E Doyle, 24 Dec 1956, L. Hubricht, 1♂; Indian Cave, 2.5 mi. SE Quebec, 23 Dec 1956, L. Hubricht, 4♂♂, 1♀; Moore Cave, 28 Oct 1969, J. Holsinger, R. Baroody, 8♂♂, 11♀♀. *Wilson Co.,* Hayes Cave, 1 mi. SE Statesville, 8 Aug 1967, S. Peck, A. Fiske, 2♂♂, 20♀♀; Jackson Cave, Cedars of Lebanon State Park, 22 Sep 1967, S. Peck, A. Fiske, 2♂♂, 6♀♀.

Diagnosis of male. — Antenna 1 esthete series uninterrupted, esthete formula from 3-0-0 to 5-0-0. Pereopod 1, palm of propodus with proximal spines, bicuspate, usually low, mesial and distal processes. Pleopod 1, protopod with 3 retinacula, exopod broadly rounded distally, slightly concave laterally, setae along distal and lateral margins, most elongate laterally. Pleopod 2 endopod tip consisting of 2 processes, cannula beak-shaped, extending perpendicular to axis of endopod, lateral process subterminal parallel to cannula, originating within margin of endopod, recurved. Pleopod exopod 4 with single sigmoid suture.

Caecidotea b. bicrenata may be distinguished from *C. b. whitei* by the position of the lateral process of the male second pleopod endopod tip. In the former subspecies, the lateral process is placed within the margin of the endopod and is recurved, often strongly, while in the latter subspecies the lateral process is found on the margin of the endopod and is straight. In mature specimens, the bicuspate processes of the propod are usually lower in *C. b. bicrenata* than in *C. b. whitei.*

Range. — Caves, from northern Alabama to northcentral Tennessee, approximately to the Cumberland River but not reaching the southern extension of the Pennyroyal plateau (Fig. 1).

Caecidotea bicrenata whitei, new combination

Asellus alabamensis. — Fleming, 1972a:247-248 (in part)
Asellus antricolus. — Fleming, 1972a: 245 (Twin Level Cave)
Caecidotea sp. no. 1. — Peck and Lewis, 1978: 44.
Caecidotea sp. no. 2. — Peck and Lewis, 1978: 44.
Caecidotea sp. — Lewis and Lewis, 1980: 23-27. — Lewis, 1981a: 21; 1981b: 234-236.
Caecidotea meisterae Lewis and Bowman, 1981: 28-32.
Caecidotea whitei Lewis and Bowman, 1981: 51-59.

Material examined. — TENNESSEE: *Davidson Co.*, Crocker Springs Cave, 12 Nov 1956, C.K. Barr, 3♂♂, 4♀♀; Nashville, 3 Mar 1901, E.B. Williamson, 6♂♂, 6♀♀. *Sumner Co.*, Escue Cave, 2 mi. NE Portland, 18 Apr 1958, L. Hubricht, 10♂♂, 17♀♀. KENTUCKY: *Edmonson Co.* , Mammoth Cave National Park, Cedar Sink Cave, 5 mi. SW Mammoth Cave, 31 Aug 1939, L. Hubricht, 3♂♂. Cave over Styx River Spring, 26 June 1981, J. Lewis, T. Lewis, 4♂♂, 1♀. Mammoth Cave: Flint Dome in Jessup Avenue, 6 Sep 1981, J. Lewis, J. Eckstein, 4♂♂, 9♀♀; Styx River, near Natural Bridge, 28 June 1980, J. Lewis, T. Lewis,

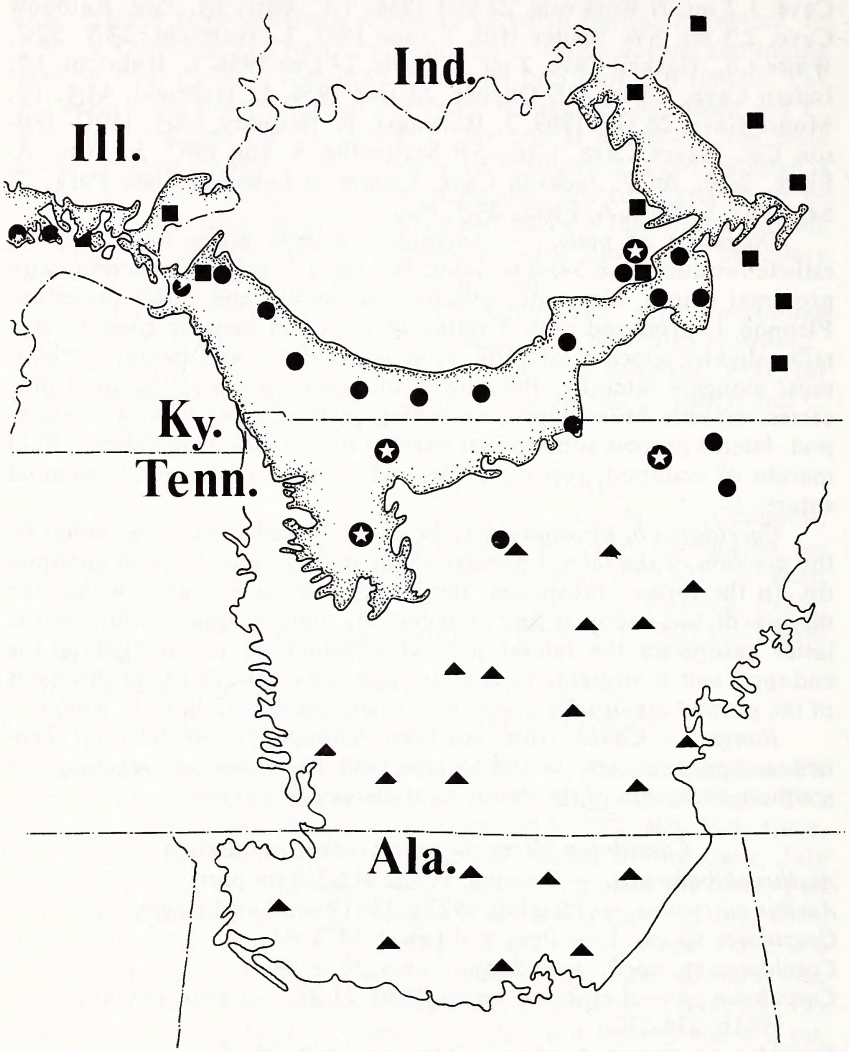

Fig. 1. Distribution of the troglobitic *Caecidotea* of the southern Interior Low Plateaus: *Caecidotea bicrenata bicrenata* (triangles); *Caecidotea bicrenata whitei* (solid circles); *Caecidotea bicrenata* unidentified subspecies, lacking lateral process on second pleopod endopod tip (stars); *Caecidotea stygia* (squares). The stippled region, which comprises most of the range of *C. b. whitei*, is the Pennyroyal Plateau.

1♂; Hawkins River, 2 Aug 1980, J. Oberlies, 5♂♂, 9♀♀; Roaring River, Shrimp Pools area, 19 Aug 1980, J. Lewis, T. Lewis, 7♂♂, 14♀♀; pools in Carlo's Way, 17 Oct 1981, J. Lewis, T. Lewis, M. Hale, 4♂♂, 3♀♀; same location, 28 Dec 1981, J. Lewis, T. Lewis, J. Eckstein, 1♂, 1♀. Parker Cave, Parker River, 20 Aug 1980, J. Lewis, T. Lewis, 8♂♂, 15♀♀. *Barren Co.*, Mill Hole, 20 Aug 1980, J. Lewis, T. Lewis, 7♂♂, 14♀♀. *Simpson Co.*, Old Smokey Cave, 20 mi. SW Bowling Green, 1 July 1981, J.R. Holsinger, 21♂♂, 19♀♀.

Diagnosis. — *Caecidotea b. whitei* can be distinguished from the nominate subspecies by the straight lateral process of the male second pleopod endopod tip of *C. b. whitei*, which is placed directly on the margin of the endopod. In mature males where both the medial and distal processes are well developed, the medial process usually appears as a large triangular process with a shoulder distally, rather than a well developed bicuspate process. This characteristic, however, is also shared with some populations of *C. b. bicrenata.*

Range. — *Caecidotea b. whitei* occurs from northcentral Tennessee north to Hart County, Kentucky, where the faulted, sandstone Hart County Ridge is apparently a barrier to its dispersal. To the west the species occurs across the Pennyroyal Plateau, from Mammoth Cave into western Kentucky, and the extension of the plateau in southern Illinois. *Caecidotea b. whitei* appears to exclude *C. stygia* in the Pennyroyal west of Mammoth Cave. In the Kentucky and Illinois counties adjacent to the Ohio River, *C. stygia* again occurs, and at least in Hardin County, Illinois, *C. b. whitei* is absent. In southwestern Illinois, *C. b. whitei* again replaces *C. stygia,* although *C. stygia* is reported from western Illinois and eastern Missouri (Fleming 1972a, b; Lewis and Bowman 1981; Peck and Lewis 1978). In the Mammoth Cave System of central Kentucky, both species occur syntopically, with *C. stygia* in small streams in the upper levels of the cave and *C. whitei* in the base level cave rivers (Lewis and Lewis 1980; Lewis 1981a)

Discussion. — In support of the synonymy of *Caecidotea meisterae* with *C. whitei,* illustrations of the gnathopods of both forms from a habitat in Mammoth Cave are given in Figure 2. Figure 3 illustrates the tip elements of male second pleopod endopods. Figure 4 illustrates male pleopod 1, and Figure 5 shows the palmar margin of the propodus of male first pereopods. Although *C. meisterae* is the more differentiated of the two forms, *C. whitei* is chosen as the senior synonym for two reasons. First, in the numerous collections examined both here and in Lewis and Bowman (1981), the morphology of *C. whitei* is by far the more prevalent and typical of the species. Second, the type-locality of *C. whitei,* Cricket Cave, is a well known but remote locality that is currently unthreatened by man. In contrast, the type-locality of *C. meisterae* in Johnson County, Illinois, lies adjacent to an active limestone quarry. Although still some distance from the cave, this quarry has already consumed one cave (Bretz and Harris 1961), and local residents believe that the quarry operations may eventually consume other sections of White Hill.

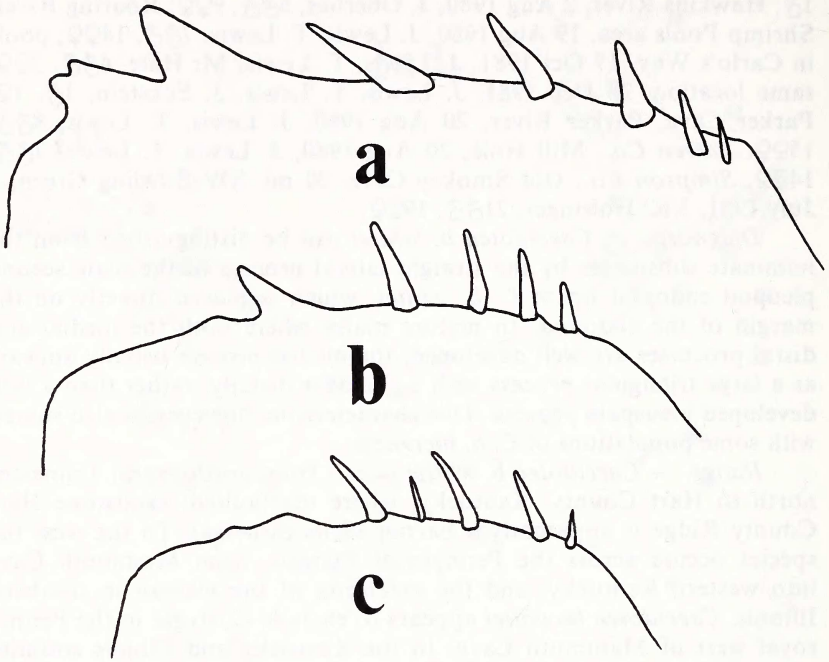

Fig. 2. Palmar margin of propodus of male first pereopods of *Caecidotea bicrenata whitei* from Roaring River Shrimp Pools, Mammoth Cave, KY: (a) 8 mm individual, *C. meisterae* form; (b) 6 mm individual, *C. whitei* form; (c) 4 mm individual, immature.

Caecidotea whitei is redefined as a subspecies of *Caecidotea bicrenata* due to the slight morphological differences that distinguish them, and the lack of dispersal barriers that might provide reproductive isolation along the contact between *C. whitei* and *C. bicrenata.* Apparently the ranges of *C. b. bicrenata* and *C. b. whitei* contracted at some time in the past, then range expansion followed. If this occurred, some secondary contact phenomenon might be expected, either hybridization or character displacement. Along the contact between the two subspecies, occasional populations occur in which the lateral process of the male second pleopod endopod tip (Fig. 3) is either vestigial or absent. Considering the close morphological similarity of the two subspecies, it seems more likely that this phenomenon is caused by breakdown of any isolating mechanisms developed, rather than reinforcement. However, without experimentally crossbreeding individuals taken from populations of each subspecies it is impossible to say with certainty that hybridization is occurring. Furthermore, the presence of specimens lacking the lateral process in one stream in Mammoth Cave (Mystic River) complicates the situation. Mammoth Cave is relatively distant from

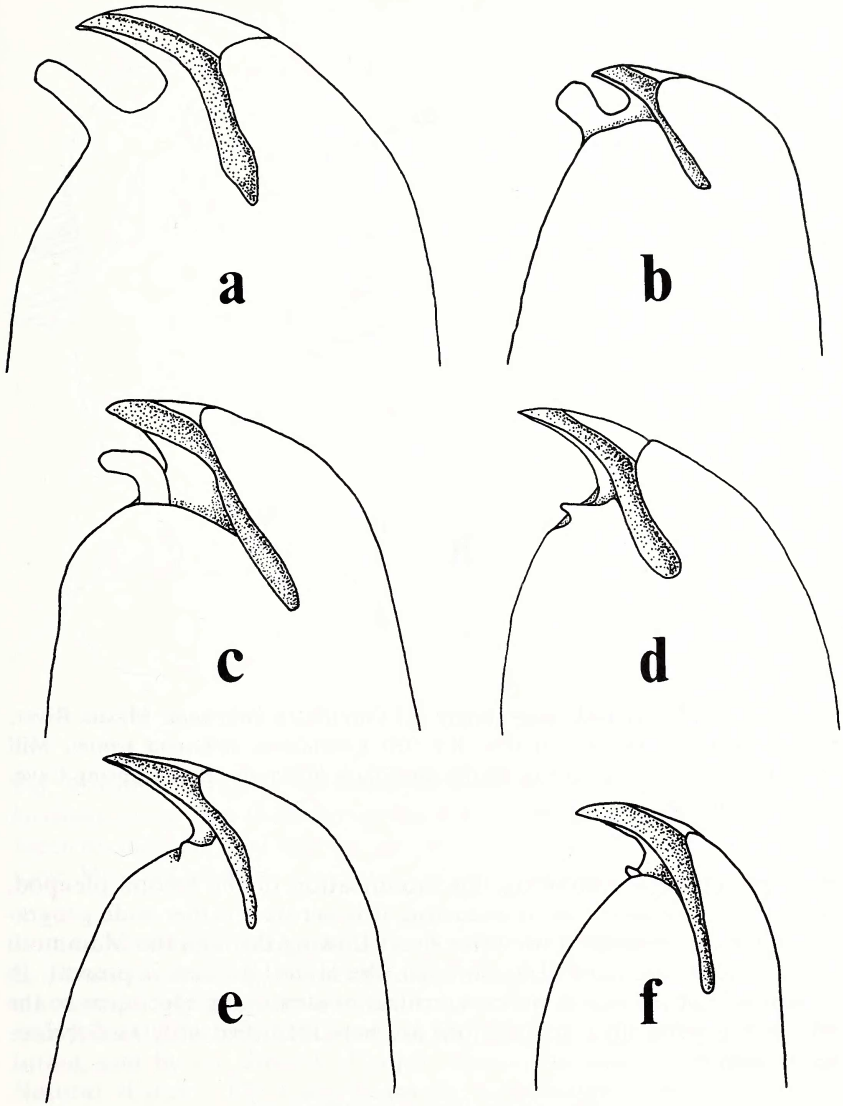

Fig. 3. Tip elements of male second pleopod endopods: (a) *Caecidotea bicrenata whitei,* Carter Cave, Jackson Co., TN; (b) *Caecidotea bicrenata whitei,* Mill Hole, Barren Co., KY; (c) *Caecidotea bicrenata bicrenata,* B&J Cave, Morgan Co., AL; (d) *Caecidotea bicrenata,* Mystic River, Mammoth Cave, Edmonson Co., KY; (e) *Caecidotea bicrenata,* Dunbar Cave, Montgomery Co., TN; (f) *Caecidotea bicrenata,* Columbia Caverns, Dickson Co., TN.

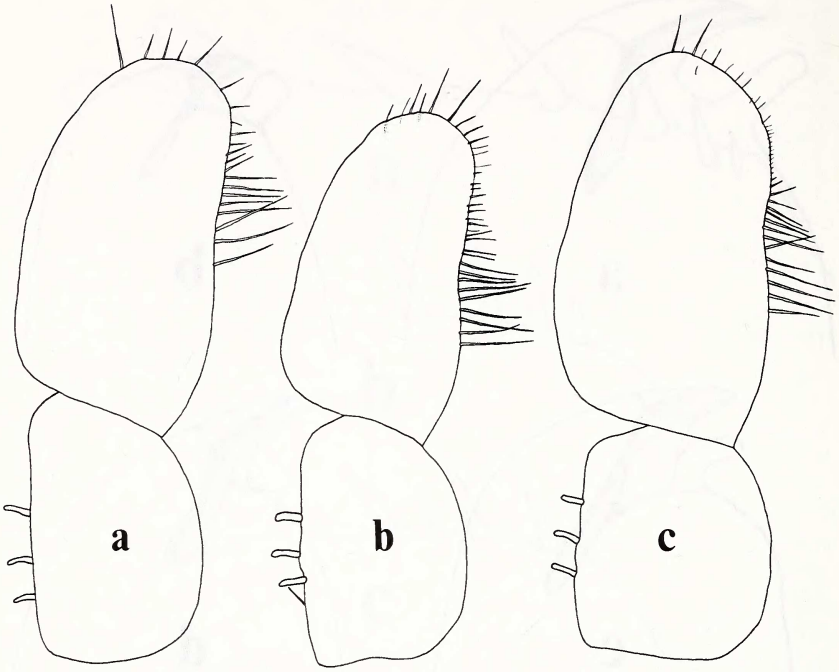

Fig. 4. Pleopod 1 of male *Caecidotea:* (a) *Caecidotea bicrenata,* Mystic River, Mammoth Cave, Edmonson Co., KY; (b) *Caecidotea bicrenata whitei*, Mill Hole, Barren Co., KY; (c) *Caecidotea bicrenata bicrenata,* Beech Spring Cave, Marshall Co., AL.

other populations exhibiting this modification of the second pleopod, such that if hybridization is occurring it is across a rather wide geographic range. In isopods from other rivers flowing through the Mammoth Cave System that have been sampled, the lateral process is present. In the absence of the lateral process, critical in identifying specimens to the subspecific level, these populations are here identified only as *Caecidotea bicrenata.*

Caecidotea bicrenata (Steeves)

Material examined. — TENNESSEE: *Dickson Co.*, stream in Columbia Caverns, 2 mi. SW VanLeer, 22 June 1957, L. Hubricht, 4♂♂, 3♀♀. *Macon Co.*, Ann White Cave, 6 mi. W Lafayette, 19 Apr 1958, L. Hubricht, 9♂♂, 7♀♀. *Montgomery Co.*, Dunbar Cave, 1.5 mi. S St. Bethlehem, 15 June 1957, L. Hubricht, 13♂♂, 1♀. KENTUCKY: *Edmonson Co.*, Mammoth Cave National Park, Mammoth Cave, Mystic River near Mystic River tributary, 27 Dec 1981, J. Lewis, T. Lewis, J. Eckstein, T. Leitheuser, 5♂♂.

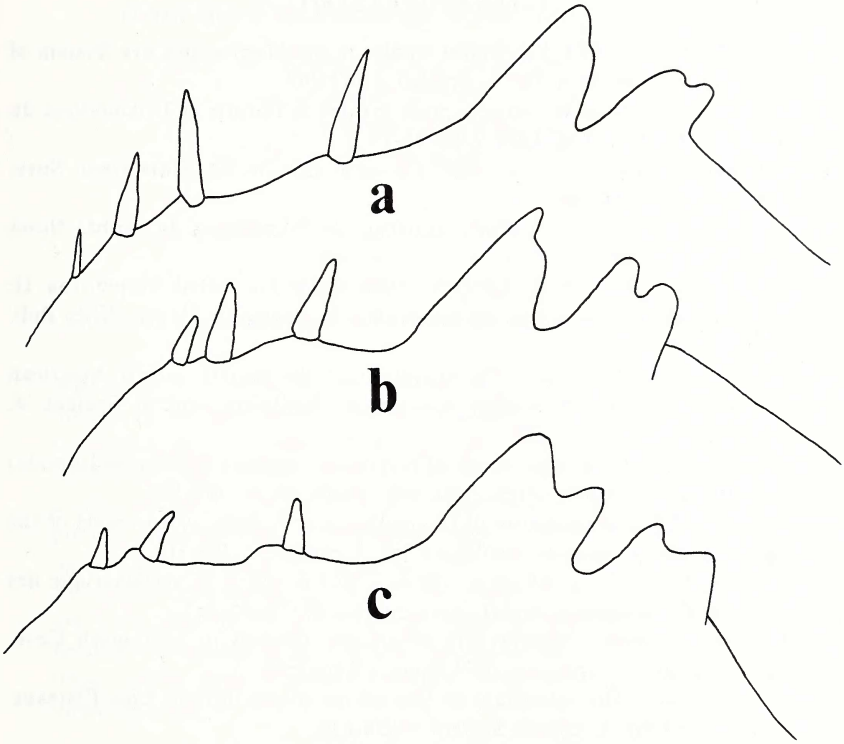

Fig. 5. Palmar margin of propodus of male first pereopods: (a) *Caecidotea bicrenata whitei,* Mill Hole, Barren Co., KY; (b)*Caecidotea bicrenata bicrenata,* Beech Spring Cave, Marshall Co., AL; (c) *Caecidotea bicrenata bicrenata,* B&J Cave, Morgan Co., AL.

ACKNOWLEDGMENTS. — I would like to thank Drs. Thomas E. Bowman, John R. Holsinger, and Gerald A. Cole for reading the manuscript. Much of the material examined was provided by Dr. Bowman from the National Museum of Natural History, Smithsonian Institution, and by Dr. John E. Cooper, North Carolina State Museum of Natural History. The Cave Research Foundation provided use of its field station in Mammoth Cave National Park, and many members of CRF aided in the collection of asellids in Mammoth Cave, especially Mrs. Teresa M. Lewis and Mr. James Eckstein. I also thank Mr. Robert Deskins, Mr. James Wiggins and the rest of the staff at Mammoth Cave National Park for their cooperation in expediting my research at Mammoth Cave. Funds were provided by a grant from the Research Advisory Committee and the 1980 Stone Graduate Research Award of the National Speleological Society, and a grant from the Graduate School of the University of Louisville. This paper is Contribution #207 (New Series) of the Department of Biology, University of Louisville.

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Accepted 12 July 1982